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A REVISION OF THE *EUPLOEA BATESII* C. & R. FELDER, 1865 'COMPLEX' (LEPIDOPTERA: NYMPHALIDAE: DANAINAE) IN MAINLAND PAPUA NEW GUINEA AND AUSTRALIA, INCLUDING ITS BIOLOGY AND BIOGEOGRAPHY

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Abstract

The biogeography, biology and taxonomy of the *Euploea batesii* C. & R. Felder, 1865 'complex' from mainland Papua New Guinea and Torres Strait were studied and all specimens examined were grouped into one of three forms or morphological types. Immature stages of the immaculate form (Morph type 1) are described and illustrated from material collected on Mer Island, Torres Strait, where the larval host plant was *Parsonsia velutina* R.Br. (Apocynaceae). On Mer Island, adults of several types were found in large numbers imbibing pyrrolizidine alkaloids from dead and damaged leaves and flowers of *Heliotropium foertherianum* Diane & Hilger (Boraginaceae). The three morphological types were found to have distinctive sympatric and allopatric distributions, which might be determined by larval host plant specificity. Broadly, all three types occur in eastern Papua New Guinea and on Mer Island in Torres Strait, while only the immaculate type is known elsewhere in New Guinea and on other Torres Strait islands. On Mer Island, captive mothers of the immaculate Morph type 1 produced final instar larvae that were charcoal black in colour and resulted in only immaculate Morph type 1 (F1) offspring; these F1 were not discernibly different from nominotypical *E. batesii* from Indonesian West Papua. The distributions of the maculated types (Morph types 2 and 3) and several other butterfly species which are only known to occur in Torres Strait on Mer Island, support a probable link in the geological history of Mer Island and eastern Papua New Guinea. In addition, the distribution of the immaculate form indicates a link in the geological history of the islands in the west of Torres Strait to the southern region of mainland Papua New Guinea. The *E. batesii* 'complex' likely includes more than one species, with perhaps more species occurring through the major islands and archipelagos along the Solomon chain east of New Guinea. Based on the distinct distributional and wing morphological differences occurring in populations in Papua New Guinea and Torres Strait, plus life history evidence, it is proposed that *E. b. resarta* Butler be revised to species status (*E. resarta* Butler, 1876, **stat. rev.**) and that *E. b. squalida* (Butler) be revised to a form of *E. resarta* (*E. resarta* f. *squalida* (Butler, 1878), **stat. rev.**), both taxa occurring together exclusively in eastern mainland Papua New Guinea and on Mer Island. Also, the immaculate monotypic populations (Morph type 1) occurring on mainland New Guinea and its outlying islands and in Torres Strait are proposed as new synonyms of *E. b. batesii.*

Introduction

Euploea batesii C. & R. Felder, 1865 is currently classed as a polytypic species found principally in the New Guinea region, *i.e.* from Buru, Seram and Ambon in the west, across New Guinea and its outlying islands, to the Solomons in the east (Ackery and Vane-Wright 1984, Parsons 1998, Tennent 2002a). South of New Guinea it extends to the Aru Islands in the Arafura Sea (Ackery and Vane-Wright 1984) and into Torres Strait in Queensland, Australia (Braby 2000). In Papua New Guinea it is widespread, occurring in marginal secondary vegetation and forests up to 1200 m (Parsons 1998). Its distribution across the bulk of New Guinea is poorly known and there are few specimens from this region in Australian collections. In Torres Strait, *E. batesii* occurs mostly in marginal, dense primary or secondary monsoon vine forest, but can frequent overgrown and abandoned village gardens.

The life history of *E. batesii* was partially described from material collected near Bulolo in Papua New Guinea by Parsons (1998), where he recorded *Parsonsia lata* Markgr. and *Hoya* R. Br. sp. (Apocynaceae) as larval hosts, while Szent-Ivany and Carver (1967) reported larvae occurring commonly on the ornamental *Nerium oleander* L. (Apocynaceae) at Port Moresby, Papua New Guinea.

Felder and Felder (1865) described the syntypes of *E. batesii* from Dodinga, Halmaheira, in the Northern Moluccas (Edwards *et al.* 2001); several authors since have expressed doubts concerning the authenticity of this type location (Ackery and Vane-Wright 1984, Parsons 1998). This uncertainty was primarily based on the fact that 'type' labels are not attached to any *E. batesii* specimens in the Felder collection (Talbot 1943) and, moreover, the *E. batesii* 'complex' is otherwise not known from Halmaheira. In addition, Ackery and Vane-Wright (1984) provided circumstantial evidence that a female syntype (in the Felder collection) was, with another syntype of *E. b. batesii*, in the same batch of Felder specimens from Ambon in the Southern Moluccas. Ambon is just west of New Guinea, from which the current designated distribution of the *E. batesii* 'complex' extends eastward to the Solomon Islands (Fruhstorfer 1910, Corbet 1942, Ackery and Vane-Wright 1984, Parsons 1998, Tennent 2002a).

Ackery and Vane-Wright (1984) listed 24 names that have been applied to *E. batesii* at various times, while D'Abrera (1978) listed 13 subspecies from the region, with four subspecies purportedly occurring on mainland Papua New Guinea (Parsons 1998). Tennent (2002a) recorded an additional five subspecies from the Solomon Islands. Corbet (1943) placed *E. batesii* in the *E. climena* (Stoll) species group, indicating that members of this group are characterised by the presence of a recurrent vein in the forewing cell and, in males, the absence of a pale raised patch in the cell of the hindwing upperside and the absence of an androconial brand on the forewing upperside. Corbet (1943) and Carpenter (1953) also pointed out that males of *E. batesii* could then be separated from their congeners within the *climena* group by possessing, on the forewing underside, an elongate white stripe in the anterior half of space 1b and a narrower white stripe below it. These stripes may be pale or dark and are also used to distinguish female *E. batesii*. Conversely, Ackery and Vane-Wright (1984), in their cladistic study of the Danainae, placed *E. batesii* in a clade separate from *E. climena* but admitted that all of the species within the same clade containing *E. batesii* were difficult to characterise. Equally, Parsons (1998) believed that the taxonomy of *E. batesii* was formidable and in need of revision, especially due to the high degree of variation recorded in wing pattern across its range and the possibility that *E. batesii* might comprise a species complex similar to other suspected complexes within *Euploea* Fabricius (Ackery and Vane-Wright 1984, De Baar 1991).

Here I review the distribution and polymorphism of the *E. batesii* 'complex' on mainland Papua New Guinea (PNG) and in Torres Strait, Australia, describe and illustrate the life history of the immaculate morph (Morph type 1) from Mer I. in eastern Torres Strait, determine the larval host plant on Mer I. and discuss its general ecology. I also document the species' known distribution on the island of New Guinea, the archipelagos east of New Guinea and in Torres Strait, and analyse and discuss the polymorphism (degree of wing spotting) of the complex from Torres Strait, mainland PNG and its outlying islands. The results of these analyses, together with life history data, are used to propose the reinstatement of *E. resarta* Butler, 1876 **(stat. rev.)**, which occurs exclusively in eastern mainland PNG, on several of its outlying islands and on Mer I. In addition, in eastern mainland PNG and on Mer I. it is proposed that this species occurs sympatrically with *E. batesii batesii*, with the latter taxon also occurring across mainland New Guinea and several of its outlying western islands and on several islands in Torres Strait.

Material and methods

Life history and ecology studies on Mer Island, Torres Strait

An extensive search was undertaken for immature stages in January 2011 along the edges of monsoon vine forest on Mer I. (9°55'S, 144°30'E) (Fig. 61), the largest of three basaltic islands collectively called the Murray Island group, which are the remains of volcanic cones (Willmott 1972). Natural vegetation consists of tropical deciduous monsoon forest. Immature stages of *E. batesii* were found only on *Parsonsia velutina* R.Br. (Apocynaceae), following which seven unspotted, dark brown to black adult females were collected and released in an abandoned shade house (2 m wide, 4 m long, 2 m high), which served as a makeshift flight cage. Long stems of the larval host plant, plus sprigs of flowering lantana (*Lantana camara* L. [Verbenaceae]), which were used as a nectar source by adults, were placed in long-necked jars of water suspended from the ceiling of the shade house using wire. All early stages collected were reared at ambient conditions in round, clear plastic food containers (volume 280 mL, height 75 mm, bottom radius 42.4 mm, top radius 55 mm). Larvae were fed on fresh host plant introduced daily. Three adults were reared from field-collected material and 14 from eggs laid in the improvised flight cage.

Analysis of specimens from mainland Papua New Guinea and Torres Strait

Specimens of the *E. batesii* 'complex', predominantly from mainland Papua New Guinea and its nearby islands (n = 92) and Torres Strait (n = 154), were examined and grouped into three morphological types, which were then further grouped relative to their collection sites. In addition, photographs of the genital armature of four dark brown to black males of *E. batesii* (from Dauan I., Torres Strait x 2; Brown R. near Port Moresby, Papua New Guinea; and Yapen, Indonesian West Papua) were compared with those of four well-spotted males (from Mer I. x 2; and Bulolo, Papua New Guinea x 2), using a stereo microscope and image stacking software (Helicon Focus 5.3®, 2012), in order to determine if morphological differences in wing pattern corresponded with any differences in genital structures, with nomenclature used following Ackery and Vane-Wright (1984) and Monastyrskii (2011).

Abbreviations of collectors' names appearing on specimen labels and collection depositories are: A&GD – A. and G. Daniels; AIK – A.I. Knight; AM – Australian Museum, Sydney; ANIC – Australian National Insect Collection, Canberra; AT – A. Tubb; CWWTC – C.W. Wyatt theft collection (AM); DKM – D.K. McAlpine; EJLH – E.J.L. Hallstrom; EM – E. Mann; GAWC – G.A. Waterhouse collection (AM); GLC – G. Lyell collection (AM); GMC – G.M. Carson; GRF – G.R. Forbes; GRFC - G.R. Forbes collection, Brisbane; GW – G. Wood; GW (ANIC) – G. Wood (Long I., -.i.1956 locality); HE – H. Elgner; HR – H. Rauber; IFTA - Insect Farming and Trading Agency, Bulolo, Morobe Province; JGG – J.G. Grimshaw; JOC – J.O. Campbell; MDB – M. De Baar; MDBC – M. De Baar collection, Brisbane; MM – Macleay Museum, Sydney; MTQ – Museum of Tropical Queensland, Townsville; MW – M. Willows jnr; N&SHC – N. and S. Hunter collection (AM); OM – O. McCaw; PSH – P.S. Hanahan; QDAFFC – Queensland Department of Agriculture, Fisheries and Forestry collection, Brisbane; QM – Queensland Museum, Brisbane; RC – R. Carver; SGC – S. Ginn collection, Sydney; SJJ&IRJ – S.J. and I.R Johnson; TAL – T.A. Lambkin; TLFC – T.L. Fenner collection, Brisbane; TLIKC – Joint collection of T.A. Lambkin and A.I. Knight, Brisbane; VRC – van Raalte collection (AM); WIP – W.I. Potter; WWB – W.W. Brandt.

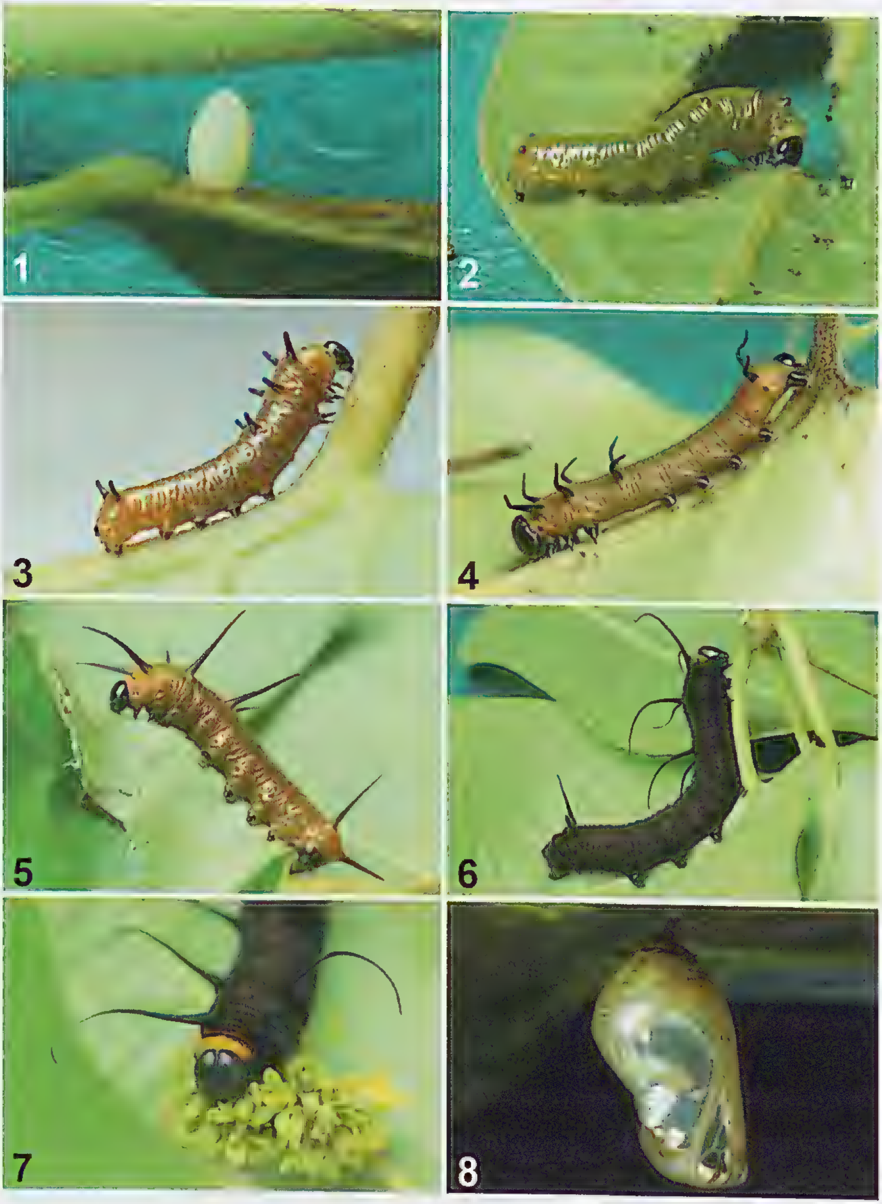
Life history and biological studies on Mer Island, Torres Strait

Host plant: *Parsonsia velutina* R.Br. (Apocynaceae).

Egg (Fig. 1): (n = 10); typical of *Euploea* spp; bullet-shaped; whitish-yellow; basal half of egg relatively smooth with outlines of square recessed dimples, 6 dimples high, each dimple outlined with vertical columns and diagonal rows; apical half of egg with hexagonal dimples, 4-5 dimples high, hexagons becoming smaller at apex; within a few days becoming yellow.

First instar larva (Fig. 2): (n = 16); head black; body cylindrical, smooth, glossy and semitranslucent; lime-green, abdominal segment 8 orange; a pair of slightly raised carmine protuberances on mesothorax, metathorax and abdominal segments 2 and 8; bases of legs and prolegs same colour as body, legs and prolegs black.

Second instar larva (Fig. 3): (n = 20); head and body similar to first instar, except body not translucent; yellow-orange; spiracles on prothorax and abdominal segment 8 black; a pair of blunt, black filaments shorter than width of body on mesothorax, metathorax and abdominal segments 2 and 8, with pair on mesothorax slightly longer than others; bases of legs and prolegs same colour as body, legs and prolegs black.



Figs 1-8. Early stages of the *Euploea batesii* 'complex' from Mer Island, Torres Strait (Morph type 1 = *E. b. batesii*): (1) egg (height 1.8 mm); (2) 1st instar larva (length 6.5 mm); (3) 2nd instar larva (14 mm); (4) 3rd instar larva (25 mm); (5) 4th instar larva (30 mm); (6) 5th instar larva (45 mm); (7) 5th instar showing prominent orange collar (45 mm); (8) pupa (height 22 mm).

Third instar larva (Fig. 4):(n = 20); similar to second instar except whole body and head tomentose; body dull in colour; filaments longer, roughly the width of the body; anal segment black; all spiracles black with those on prothorax and abdominal segment 8 larger than others.

Fourth instar larva (Fig. 5): (n = 20); similar to third instar except body glossy and semi-translucent; filaments longer, roughly 1.5 x width of body.

Fifth instar larva (Figs 6-7): (n = 18); similar to fourth instar except entire body and head tomentose; body, including filaments, dull charcoal-black except for a semi-circular bright orange dorsal collar on prothorax; head, legs, prolegs and spiracles glossy black; all filaments roughly twice the width of the body.

Pupa (Fig. 8): (n = 18); typical of *Euploea* spp; entirely amber at first; after 2 days abdomen, wing cases, thorax, eyes and antennae change to shining silver; buff markings on abdomen and wing-cases; spiracles pale brown.

The early stages of the *E. batesii* 'complex', specifically of the black immaculate form, were discovered on *P. velutina*, as per Stanley and Ross (1986) and Harden *et al.* (2007). *Parsonsia velutina* was the only *Parsonsia* species found on the island. Overall, the early stages were difficult to find as the host plant predominantly grew out of reach, high in the forest canopy (Fig. 9). Eventually, eggs and early instar larvae were found on two large vines, only on the soft growing tips of the host plant, but larger larvae were found on, and fed freely on, the harder, more mature leaves and, when ultimate, fed on flower buds and racemes (Figs 7, 9). Interestingly, final instar larvae superficially resemble, in both colour and form, final instar larvae of *Ornithoptera priamus poseidon* (Doubleday, 1847) (Lepidoptera: Papilionidae), which also occurs on the island.

During the wet season in Torres Strait (normally between December and April), adults of *E. batesii* are frequently observed on Mer I., where they regularly nectar throughout the day from *Lantana camara*, often with *E. algea amycus* Miskin, 1890 and *E. tulliolus tulliolus* (Fabricius, 1793). In addition, males of all three *Euploea* spp, as well as males of *Tirumala hamata hamata* (W.S. Macleay, 1826), were found throughout the day, frequently in large numbers, imbibing pyrrolizidine alkaloids from dead and damaged leaves, and flowers, of *Heliotropium foertherianum* Diane & Hilger (Boraginaceae) (known also as the heliotrope tree, *Tournefortia argentea*) (Figs 10-11) growing in sand on beaches and behind dunes (Fig. 12). Similarly, adults of *T. h. hamata* were also found to be attracted to flowers and leaves of *Crotalaria retusa* L. (Fabaceae). Females of *E. batesii* were often observed flying along margins of vine thickets, in undergrowth and through abandoned gardens, but were generally secretive and rarely observed when ovipositing. Overall, the adult butterflies have a slow, gliding flight with long wing beats.

Figs 9-10. (9) *Parsonsia velutina* (Apocynaceae): host plant of the *Euploea batesii* 'complex' (Morph type 1 = *E. b. batesii*) on Mer Island, Torres Strait; (10) adults of the *Euploea batesii* 'complex' (Morph type 1 = *E. b. batesii*) clustered with *E. algea amycus*, *E. tulliolus tulliolus* and *Tirumala hamata hamata* imbibing pyrrolizidine alkaloids from stems and dead leaves of *Heliotropium foertherianum* (Boraginaceae).

Figs 11-12. (11) Damaged leaves and immature fruit of *Heliotropium foertherianum* (Boraginaceae), Mer Island, Torres Strait; (12) mature *H. foertherianum* growing on sand with swarming adults of *Euploea* spp and *T. tirumala* imbibing pyrrolizidine alkaloids.

Caged females commenced ovipositing 24 hr after being released into the flight cage. All mature larvae that were reared (*i.e.* collected directly from the field off *P. velutina* and from caged mothers) were as illustrated in Figs 6-7. These larvae showed no variation in morphology or colour. In addition, all successfully reared offspring (F1) (n = 17) (*e.g.* Figs 13-14) originating from these larvae were similar (n = 14) in markings to their mothers (n = 7) (*e.g.* Fig. 15) that were released into the flight cage, *i.e.* dark brown to black, devoid of white spotting (immaculate, Morph type 1 form). Overall, mothers and reared F1 were not discernibly different from what could be considered nominotypical *E. batesii* from Yapen in Indonesian West Papua (Fig. 16).

Taxonomy

Material examined or reviewed

QUEENSLAND: 1♂, Cape York (Lectotype of *E. b. belia* Waterhouse & Lyell, 1914; illustrated in Waterhouse and Lyell [1914] Fig. 10); 1♀, Cape York, ex GAWC (AM); 1♂, 1♀, Australia (MM); QUEENSLAND (TORRES STRAIT): 1♂, Mer (or Murray) Island, 5.ix.1907 ex GAWC, passed through CWWTC, 1946-47 (AM); 15♂♂, 7♀♀, same data except 29.iii-4.iv.1986, TAL (TLIKC); 1♀, same data except (QM); 9♂♂, 6♀♀, same data except 22-25.iv.1989 (TLIKC); 29♂♂, 13♀♀, same data except 13.i.1994 (2♂♂), 14.i.1994 (2♂♂), 15.i.1994 (2♂♂), 12.v.1994 (1♂), 9.iii.1995 (6♂♂, 6♀♀), 28.i.2011 (4♂♂, 1♀), 29.i.2011 (7♂♂, 3♀♀), larva coll. 29.i.2011 (1♂), em. 6.ii.2011 (1♀), em. 20.ii.2011 (1♀), em. 1.iii.2011 (1♂), em. 4.iii.2011 (1♀), em. 5.iii.2011 (1♂), em. 11.iii.2011 (1♂), em. 18.iii.2011 (1♂) TAL (TLIKC); 6♂♂, 7♀♀, same data except TAL & AIK 25.i.2011 (3♂♂, 1♀), 26.i.2011 (2♂♂, 5♀♀), 29.i.2011 (1♂, 1♀); 7♂♂, 2♀♀, same data except AIK 25.iv-5.v.1999 (6♂♂, 2♀♀), 27.iii.2000 (1♂); 1♀, same data except 30.iii.1986 (QM); 13♂♂, 12♀♀, same data except 29.iii-4.iv.1986, MDB (MDBC); 1♂, 1♀, same data except (TLFC); 3♂♂, same data except (QM); 2♂♂, 1♀, same data except 26.iv.1984 (1♀), 30.iv.1984 (1♂), 3.v.1984 (1♂), GW (QM); 1♀, Erub (or Darnley) Island, ex GAWC, passed through CWWTC, 1946-47 (AM); 1♂, Iama (or Yam or Turtleback) Island, 7.iv.1987, MDB (TLIKC); 1♀, same data except 11-12.vi.1992, AIK; 4♂♂, 1♀, Dauan Island, 20.ii.2004 (1♂), 6.i.2006 (3♂♂, 1♀) TAL (TLIKC); 6♂♂, 1♀, same data except AIK 18.xii.2005 (1♂), 21.xii.2005 (1♂), 24.xii.2005 (1♂), 29.xii.2009 (1♂), 16.i.2004 (1♂), 2.i.2010 (1♂), 16.i.2011 (1♀); 1♀, same data except 09.22S, 142.39E, 2-4.iii.2013, SJJ&IRJ (MTQ).

PAPUA NEW GUINEA [Province names abbreviated as in Table 1]: 1♀, Aitape [SP], 26.viii.1944, JOC (VRC), (AM); 1♂, Angoram [ESP], 20 ft, 28.iv.1950, WB & EJLH (ANIC); 1♂, Balamuh [WP], 9.v.1992 JGG (QDAFFC); 2♂♂, 3♀♀, Brown River, nr Port Moresby [CP], 30.vii.1968 (1♂), 18.x.1968 (1♀), 20.x.1968 (1♀), 18.i.1976 (1♀), 28.i.1976 (1♂) GRF (GRFC); 6♂♂, 2♀♀, same data except 17.xii.1967, 26.ii.1968, 7.iv.1968, 17.vi.1968, 15.viii.1968, 23.ix.1968, 1.xi.1967 (1♀), 11.ii.1968 (1♀) HR (QM); 8 ♂♂, 6♀♀, Bulolo [MP], -.x.1984 (1♂, 1♀), -.xii.1984 (2♀♀), -.i.1985 (1♂, 1♀), -.iii.1985 (1♂), -.v.1985 (4♂♂, 1♀), -.ii.1987 (1♀), -.vii.1987 (1♂) IFTA (MDBC); 2♂♂, same data except 11.viii.1980, -.vi.1991 (SGC); 2♂♂, Erora Creek, nr Oro Bay [OP], -.v.1943, -.vi.1943 AT (AM); 1♀, Kapa Kapa [CP], 16.iv.1972 GRF (GRFC); 2♂♂, same data except 20.xi.1967, 7.iv.1968 HR (QM); 1♂ Lae, [MP], 1.xi.1973 GRF (GRFC); 1♂, same data except 24.xii.1963

(DKM); 11♂♂, 1♀, same data except 4.vi.1951 (1♂), 12.vi.1951 (1♂), 17.ix.1951 (1♂), 18.ix.1951 (1♂), 20.ix.1951 (1♂), 30.ix.1951 (1♀), 2.x.1951 (1♂), 3.x.1951 (1♂), 4.x.1951 (1♂), 10.x.1951 (2♂♂), 21.x.1951 (1♂), (WB & EJLH) (ANIC); 2♀♀, Langemak [MP], 20.iii.1944, 24.iii.1944, JOC (VRC), (AM); 1♂, Laloki River, nr Port Moresby [CP], -.vi.1943, AT (AM); 1♂, 1♀, Long I., [MBP], -.i.1956 GW (ANIC); 1♀ Morobe G [MP], WIP (AM); 1♂, Mt. Lamington Dist., Northern Division [OP], -.vii.1927, (AM); 3♀♀, Munum Waters, 15 ml W of Lae [MP] 18.i.1971, A&GD (AM); 1♂, Paga Hill, Port Moresby [CP], 15.viii.1966 EM (QM); 2♂♂, 2♀♀ Port Moresby, [CP], 20.i.1927 (1♂), 27.iii.1927 (1♂), 28.i.1927 (2♀♀) (AM); 2♂♂, same data except no date RC (AM); 1♂, same data except 'purchased for Gerrard' (AM); 1♀, same data except 20.ii.1966 RC (AM); 2♂♂, same data except 28.iii.1964, 23.v.1965 HR (QM); 1♂, same data except 7.vi.1964 HR (QM); 1♀, same data except no date HR (QM); 1♂, Rigo [CP], 28.xi.1965 HR (QM); 4♂♂, 3♀♀, Sambio Mumeng [MP], -.i.1983 (♂), -.xii.1984 (1♂), -.i.1985 (♂, 3♀♀), -.iii.1985 (♂) IFTA (MDBC); 1♂, Sambio [MP] PNG, 20.xii.1980 (SGC); 1♂, Sogeri [CP], 12.i.1968 GRF (GRFC); 2♂♂, 2♀♀, Subitana, 1800 ft [CP], 11.xii.1949 (1♂), 12.xii.1949 (1♂, 1♀), 14.xii.1949 (1♀) WWB & EJLH (ANIC); 3♂♂, Wakaiuna, Sewa Bay, Normanby I. [MBP] 23.x.1956-11.i.1957 WWB (ANIC); 1♂, Wau [MP], 1200m, -.iv.1974, collection PSH (MDBC); 1♂ (*E. batesii resarta*) Nivani Island, Louisiade Archipelago [MBP], GMC, 5.iv.1912, illustrated in: Carpenter (1953), Plate 5, Fig. 5.

SOLOMON ISLANDS: 1♂ (*E. batesii kunggana* Holotype), Kunganna Bay, Rennell Island [Rennell and Bellona Province], Templeton-Crocker expedition, MW, 6.vi.1933, illustrated in Carpenter (1953), Plate 5, Fig. 1; 1♀ (*E. batesii kunggana* paratype), same data except illustrated in Carpenter (1953), Plate 5, Fig. 4.

INDONESIAN WEST PAPUA: 2♂♂, Yapen Island, Irian Bay, -.x.1995, -.x.1997 (MDBC); 1♂ Wangaar, Irian Jaya, illustrated in: Ackery and Vane-Wright (1984), Fig. 272, p 384.

MOLUCCAS: 1♀, Buano Island, W. of Seram, Jan-Feb.1992 (MDBC).

Analysis of morphological types

For analyses, all specimens were grouped into three morphological types, illustrated in monochrome in Figs 13-36.

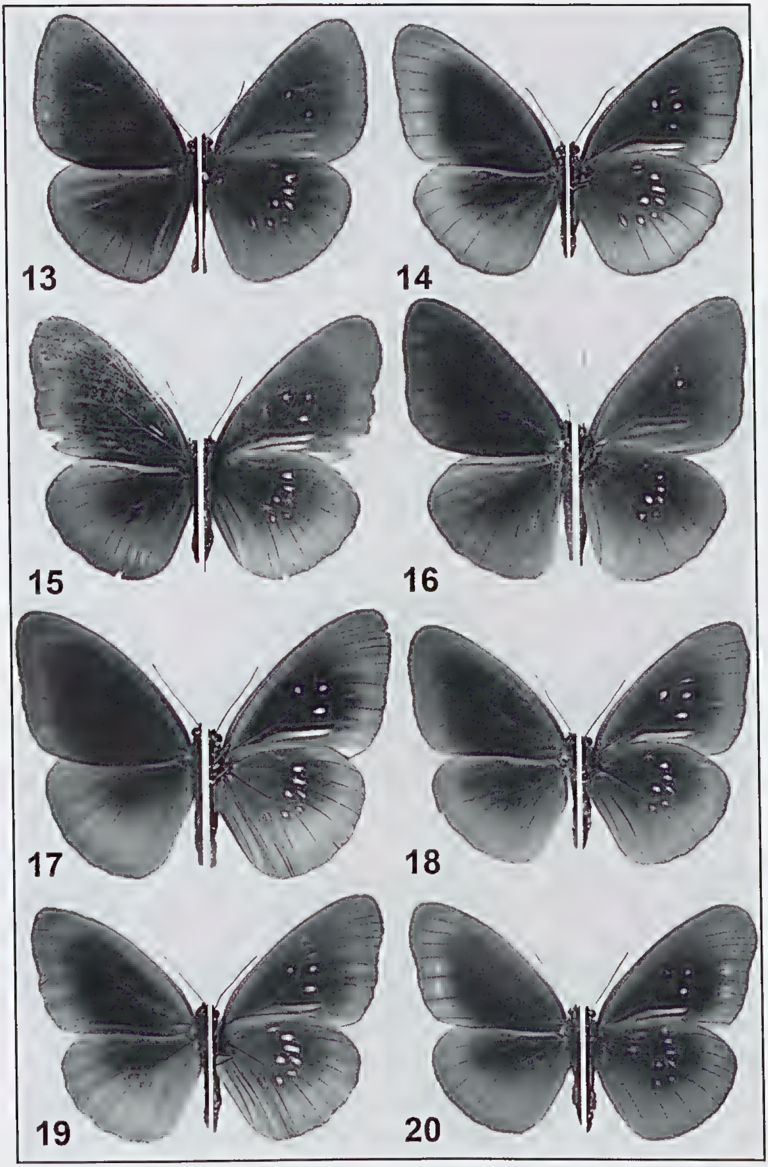
Morph type 1: Taxon *batesii*

Euploea batesii C. & R. Felder, 1865: 331.

> *E. b. batesii* (Fruhstorfer 1910: 232); *E. b. batesii* (D'Abrera 1978: 179); *E. b. batesii* (Ackery and Vane-Wright 1984: 234); *E. b. batesii* (Parsons 1998: 520); *E. b. batesii* (Edwards, Newland and Regan 2001: 311).

Euploea batesii belia Waterhouse & Lyell, 1914: 22.

> *E. b. belia* (Waterhouse 1932: 78); *E. b. belia* (Carpenter 1953: 88); *E. b. belia* (Common 1964: 58); *E. b. belia* (McCubbin 1971: 14); *E. b. belia* (Common and Waterhouse 1972: 225); *E. b. belia* (D'Abrera 1978: 178); *E. b. belia* (Common and Waterhouse 1981: 308); *E. b. belia* (Ackery and Vane-Wright 1984: 234); *E. b. belia* (Scheermeyer 1999: 192); *E. b. belia* (Edwards, Newland and Regan 2001: 311).



Figs 13-20. *Euploea batesii* 'complex', Morph type 1 = *E. b. batesii* (all figures not to scale, upper side left, under side right): (13, 16, 17) males: (13) Mer I., Torres Strait, em. 11.iii.2011, TAL, F1 [forewing length 40 mm]; (16) Yapen, Irian Bay, 1995, [44 mm]; (17) Murray (Mer) I., Torres Strait, 22-25.iv.1989, TAL, [43 mm]; (14, 15, 18-20) females: (14) Mer I., em. 4.iii.2011, TAL, F1 [39 mm]; (15) Mer I. (mother), 29.i.2011, TAL, [46 mm]; (18) Mer I., em. 6.iii.2011, TAL, [43 mm]; (19) Murray I., 9.iii.1995, TAL, [46 mm]; (20) Mer I., 29.i.2011, TAL, [46 mm].

Wings, upper and underside, dark brown to black ground colour; all wings with varying degrees of pale outer margins, especially on underside; upper and undersides of wings almost always devoid of marginal white spotting (Figs 13-20).

Morph type 2: Taxon *resarta*

Euploea resarta Butler, 1876: 241.

Crastia resarta (Butler 1878: 298); *E. resarta* (Fruhstorfer 1910: 234); *E. batesii resarta* (Carpenter 1953: 88); *E. b. resarta* (D'Abrera 1978: 178); *E. b. resarta* (Ackery and Vane-Wright 1984: 234); *E. b. resarta* (Wood 1987a: 39); *E. b. resarta* (Lambkin and Knight 1990: 108); *E. b. resarta* (Parsons 1998: 520); *E. b. resarta* (Braby 2000: 611); *E. b. resarta* (Edwards, Newland and Regan 2001: 311); *C. resarta* (Edwards, Newland and Regan 2001: 311).

As for Morph type 1, except, not all individuals with pale outer margins and upper and underside with bright, white subterminal bars, with or without white terminal spots, including bright, white subapical forewing bars, all variable in size; spotting ranging from predominantly on hind wing only and sometimes forewing only, to being present on all wings (Figs 21-28).

Morph type 3: Taxon *squalida*

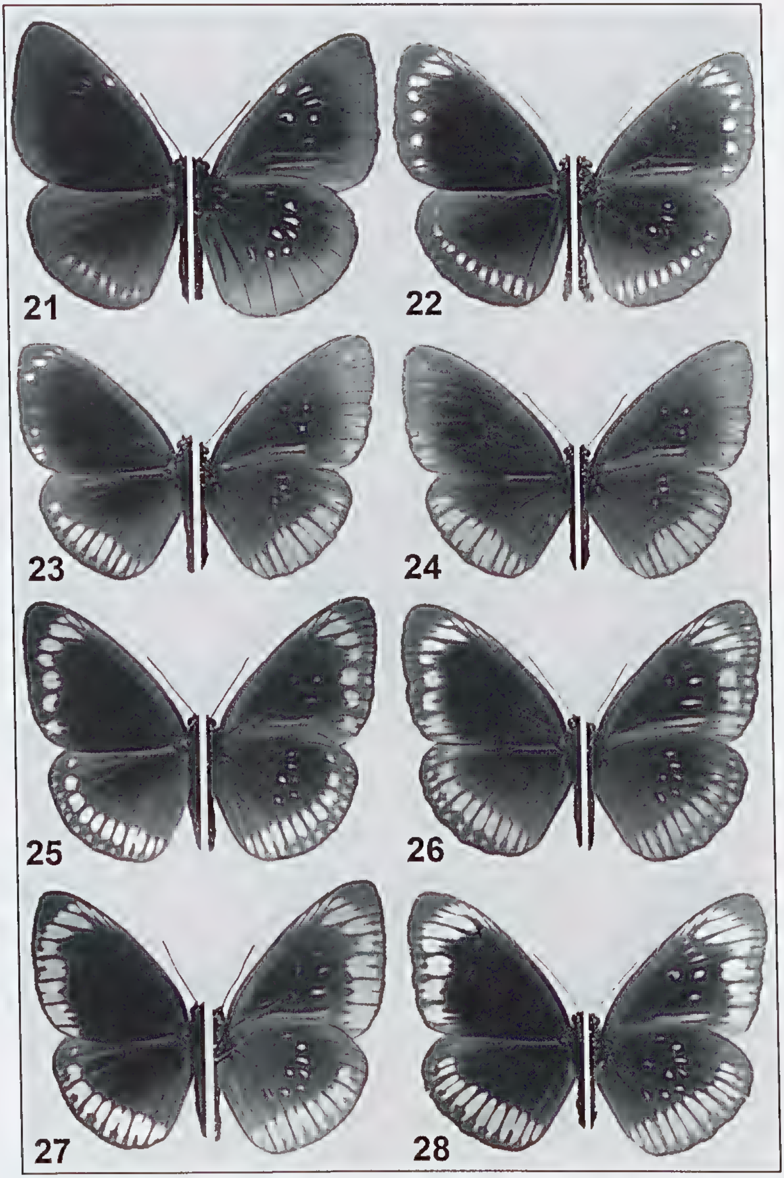
Crastia squalida Butler, 1878: 298.

Euploea squalida (Fruhstorfer 1910: 235); *E. batesii squalida* (Carpenter 1953: 88); *C. squalida* (Edwards, Newland and Regan 2001: 311).

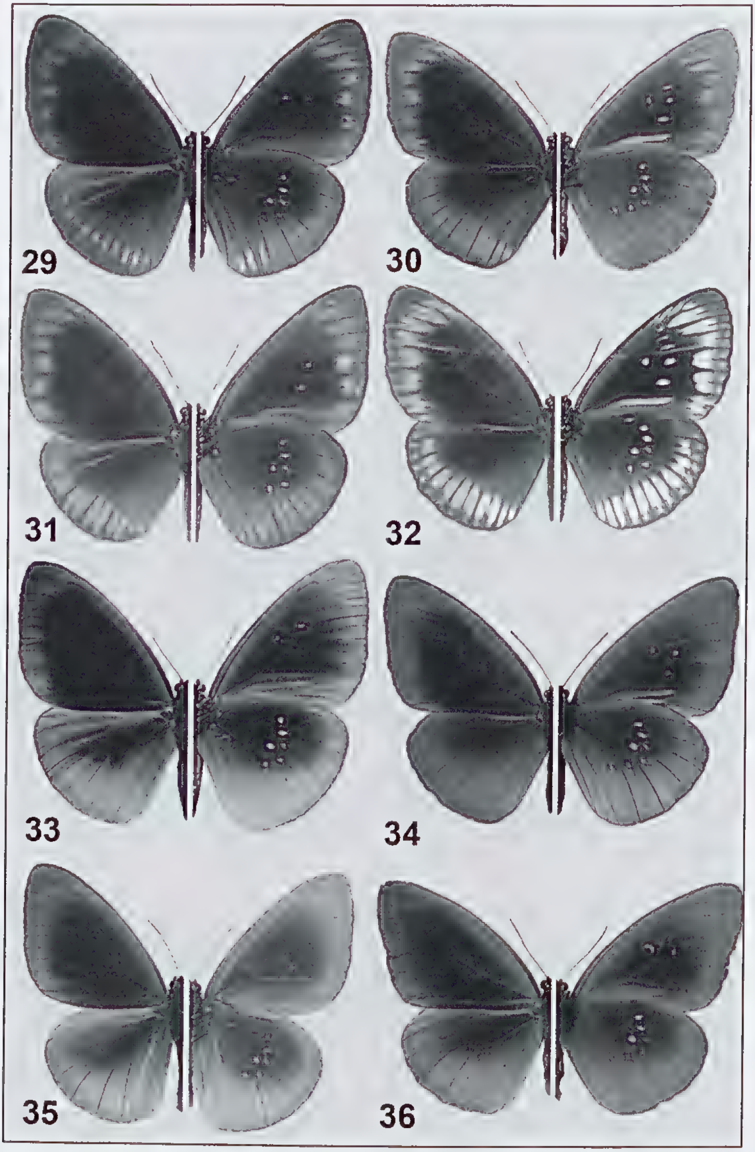
As for Morph type 2, except spots and bars overlaid variably with dark ground-colour scales, giving them a smoky appearance; Corbet (1942) referred to this as 'obsolescence of the white spots' (Figs 29-32).

Carpenter (1953) grouped the *E. batesii* 'complex' in table format, assembling each taxon based on essentially similar layouts of spots as in this revision (Table 1), *i.e.* groupings based on absence (Morph type 1), or presence of 'admarginals' (terminal spots) and 'submarginals' (submarginal and subterminal spots and bars) (Morph type 2). In addition, Carpenter (1953) categorised the other group (Morph type 3) as having 'obsolescence of the white spots' and having 'faint indications of submarginals'.

The review of specimens and their data (Table 1) showed that all those from Australia were from Torres Strait, except for a pair of doubtful origin purportedly collected at Cape York (Table 1). Of the Torres Strait specimens examined, the majority were from Mer I. (138 of 154), where it occurs as a polymorphic population ranging from dark brown or black, predominantly immaculate individuals without white spotting [Morph type 1 (*E. b. batesii*-like: Figs 13-15, 17-20) (61 of 138; 44.2% of specimens examined)], to specimens with variable amounts of bright white spots [Morph type 2 (*E. b. resarta*-like: Figs 21-28) (55 of 138; 39.9% of specimens examined)],



Figs 21-28. *Euploea batesii* 'complex' from Torres Strait, Morph type 2 = *E. resarta* **stat. rev.** (all figures not to scale, upper side left, under side right): (21-23, 25, 27) males: (21) Mer I., 25.i.2011, TAL & AIK, [forewing length 42 mm]; (22) Mer I., 29.i.2011, TAL & AIK, [44 mm]; (23) Murray (Mer) I., 29.iii-4.iv.1986, TAL, [44 mm]; (25) Murray I., 25.iv-5.v.1999, AIK, [46 mm]; (27) Murray I., 9.iii.1995, TAL, [45 mm]; (24, 26, 28) females: (24) Murray I., 29.iii-4.iv.1986, TAL, [43 mm]; (26) Murray I., 9.iii.1995, TAL, [46 mm]; (28) Murray I., 9.iii.1995, TAL, [46 mm].



Figs 29-36. *Euploea batesii* 'complex' from Torres Strait. (29-32) Morph type 3 = *E. resarta* Butler, form *squalida* **stat. rev.** (all figures not to scale, upper side left, under side right): (29, 31) males: (29) Mer I., 26.i.2011, TAL & AIK, [forewing length 42 mm]; (31) Murray (Mer) I., 22-25.iv.1989 TAL, [43 mm]; (30, 32) females: (30) Murray I., 29.iii-4.iv.1986, TAL, [41 mm]; (32) Mer I., 26.i.2011, TAL & AIK, [42 mm]. (33-36) Morph type 1 = *E. b. batesii*: (33, 35) males: (33) Dauan I., 8.i.2006, TAL, [45 mm]; (35) Yam (Iama) I., 7.iv.1987, MDB, [43 mm]; (34, 36) females: (34) Dauan I., 20.ii.2004, TAL, [40 mm]; (36) Yam I., 11-12.vi.1992, AIK, [43 mm].

Table 1. Specimens of the *E. batesii* 'complex' collected from Torres Strait, Queensland and mainland Papua New Guinea (including Long and Normanby Islands), grouped into one of three morphological categories (Morph types 1-3), relative to collection locations (Papua New Guinea collection locations listed roughly west to east in descending order).

Collection location data	Specimens in each morphological category		
	Morph type 1	Morph type 2	Morph type 3
'Australia'	1♂, 1♀[+] (MM)	-	-
Cape York, Qld	1♀ (AM)	-	1♂ (AM)[*][+]
Erub (Darnley) I., TS	1♀ (AM)	-	-
Mer (Murray) I., TS	1♂ (AM)	-	-
Mer (Murray) I., TS	41♂♂, 19♀♀	35♂♂, 20♀♀	14♂♂, 8♀♀
Dauan I., TS	9♂♂, 4♀♀	-	-
Iama (Yam) I., TS	1♂, 1♀	-	-
Balamuh, WP	1♂	-	-
Orokolo, GP	W&L	-	-
Aitape, SP	1♀	-	-
Angoram, ESP	1♂	-	-
Long I., MP	-	2♂♂	-
Langemak, MP	2♀♀	-	-
Lae, MP	3♀♀	13♂♂, 1♀	-
Bulolo, MP	1♂, 1♀	7♂♂, 6♀♀	2♂♂
Wau, MP	-	1♂	-
Sambio, MP	-	3♂♂, 3♀♀	2♂♂
Port Moresby, CP	3♂♂, 4♀♀	6♂♂	-
Brown R, Port Moresby	4♂♂, 1♀	2♂♂, 2♀♀	2♂♂, 2♀♀
Kapa Kapa, Port Moresby	1♂, 1♀	1♂	-
Sogeri, Port Moresby	1♂	-	-
Laloki R., nr Port Moresby	1♂	-	-
Subitana, CP	2♂♂, 2♀♀	-	-
Rigo, CP	1♂	-	-
Mt Lamington, OP	-	1♂	-
Erora Ck, nr Oro Bay, OP	-	2♂♂	-
Normanby I., MBP	-	3♂♂	-

Papua New Guinea provinces are: CP = Central; ESP = East Sepik; GP = Gulf; MBP = Milne Bay; MP = Morobe; OP = Oro; SP = Sandaun; WP = Western.

AM = Australian Museum, Sydney; MM = Macleay Museum, Sydney; Qld = Queensland; TS = Torres Strait; W&L = citation from Waterhouse and Lyell (1914).

*Lectotype of *E. b. belia* Waterhouse & Lyell; [+]illustrated in Waterhouse & Lyell (1914).

including an intermediate morph with 'obsolescent white spots' [Morph type 3 (closest to *E. b. squalida*-like: Figs 29-32) (22 of 138; 15.9% of specimens examined)]. In addition to Mer I., specimens of the *E. batesii* 'complex' are known in Torres Strait in the east from one historical specimen collected from Erub Island (Morph type 1) (Table 1); elsewhere in Torres Strait from Dauan Island (Fig. 62) in the north-west (13 specimens known, all of which are Morph type 1) (Figs 33-34); and just two specimens known further south in the central western part of the Strait from Iama Island (Fig. 63) (also Morph type 1) (Figs 35-36). Moreover, one of the two historical specimens purportedly from Cape York is Morph type 1, while the other is Morph type 3. This latter specimen, a male, is believed to be the Lectotype of *E. b. belia* (Peters 1971) and was illustrated in Waterhouse and Lyell (1914: fig. 10) (Table 1).

The review of specimens from mainland Papua New Guinea (including specimens from Long [MP] and Normanby [MBP] Islands: Fig. 37; Table 1), together with the Orokolo locality reference from Waterhouse and Lyell (1914) (92 records in total), plus the eastern Papua New Guinea locality references in Carpenter (1953) and Ackery and Vane-Wright (1984), showed that populations from the east of mainland Papua New Guinea (85 specimens examined) exhibited a high degree of polymorphism, similar to that seen in the population from Mer I.. Specifically, this eastern zone of Papua New Guinea, containing these mixed populations, forms a broad, almost longitudinal area running from the Astrolabe Bay and Long Island region (Madang Province) in the north to Oro Bay (Oro Province) and Rigo (Central Province) in the south, including the D'Entrecasteaux Islands (Goodenough, Fergusson and Normanby Islands: Milne Bay Province), which then stretches south-east along the Louisiade Archipelago in the south of the Solomon Sea (Fig. 37). Morph type 2 is known to the east of the Louisiade Archipelago solely on Rennell I., the southernmost island of the Solomon Archipelago (Fig. 37).

Specimens from eastern mainland Papua New Guinea therefore included all three morph types, *i.e.* Morph type 1 (30 of 85: 35.3% of specimens examined), Morph type 2 (47 of 85: 55.3% of specimens examined) and Morph type 3 (8 of 85: 9.4% of specimens examined), similar to the proportions of each type observed on Mer I. Interestingly, all Morph type 3 specimens examined from Australia and mainland Papua New Guinea, except the Lectotype of *E. b. belia* [allegedly collected on Cape York], were either from Mer I. or the zone of polymorphism in the far east and south-east of mainland Papua New Guinea (Fig. 37). The small number of specimens (4) recorded from the western and southern parts of Papua New Guinea (Aitape, Angoram, Balamuh and Orokolo: Table 1) (Fig. 37) were all Morph type 1, *i.e.* immaculate, brown to black in colour and devoid of white spotting on the uppersides of the wings.

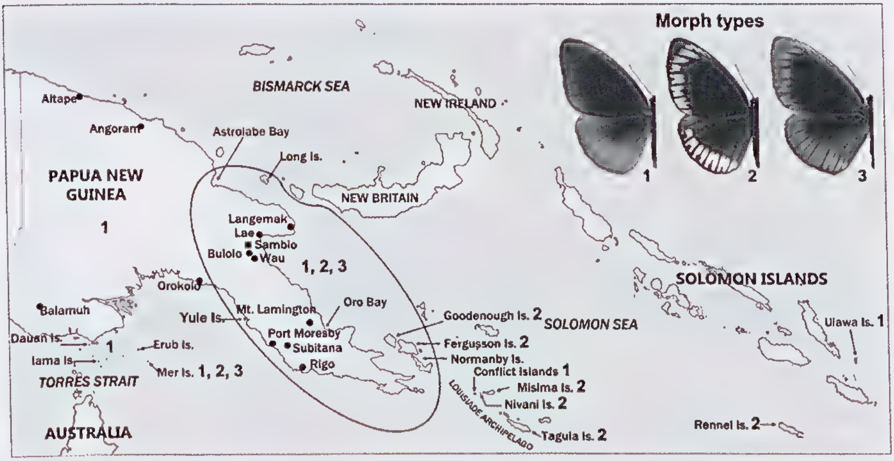
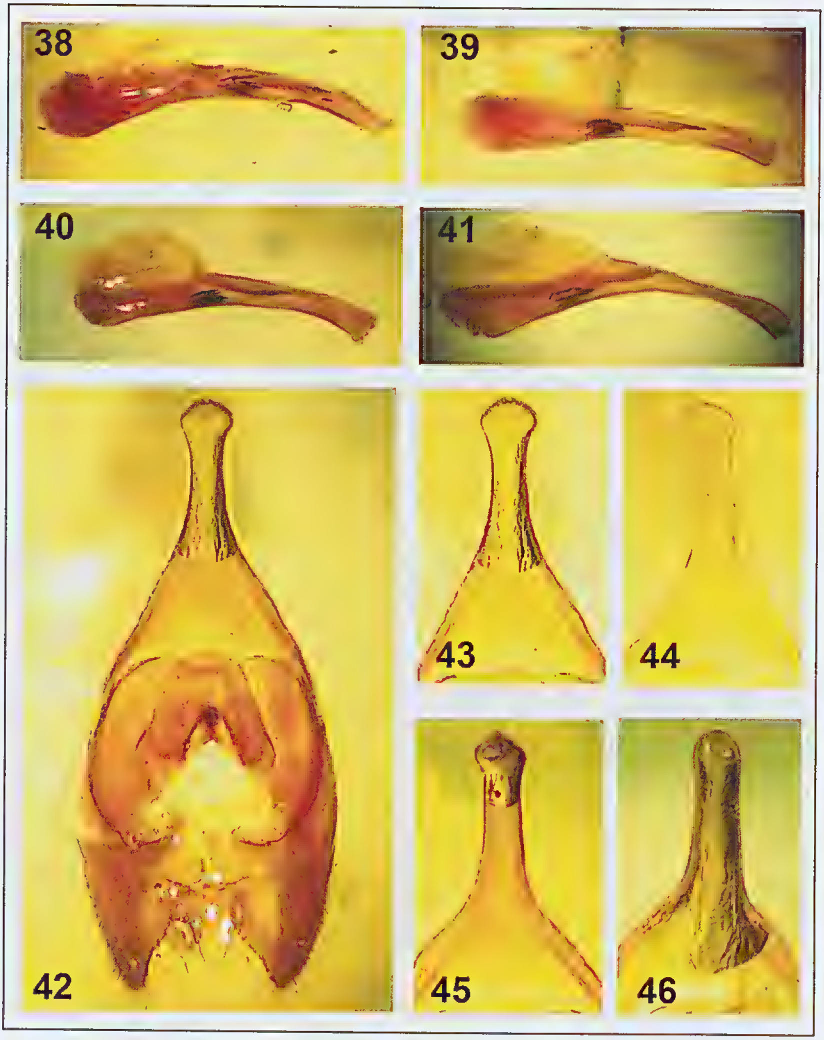


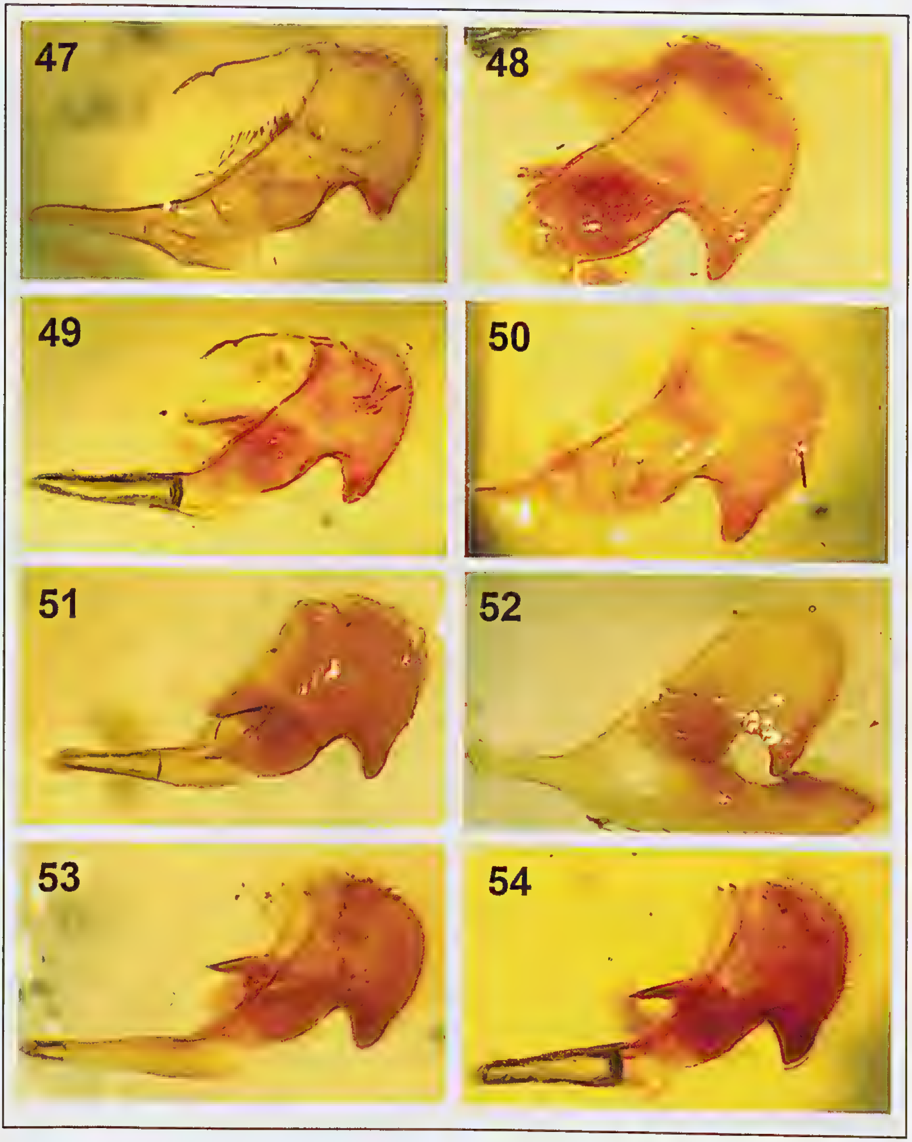
Fig. 37. Map of Papua New Guinea, Solomon Islands and northern Queensland, Australia, showing the known distributions of *E. b. batesii* (Morph type 1), *E. resarta* **stat. rev.** (Morph type 2) and *E. resarta* form *squalida* **stat. rev.** (Morph type 3). Morphological characters of populations in the area bounded in eastern mainland Papua New Guinea (except Goodenough and Fergusson Islands [Ackery and Vane-Wright 1984]) and Torres Strait were derived from museum specimens. Morphological characters of populations from western mainland Papua New Guinea were based on museum specimens plus Fruhstorfer (1910), Barrett and Burns (1951), Carpenter (1953), Ackery and Vane-Wright (1984) and Parsons (1998). Other arrowed island locations were based on Carpenter (1953), Ackery and Vane-Wright (1984), Parsons (1998) and Tennent (2001, 2002a).

Examination of the genital armature, in particular the phallus (Figs 38-41), saccus (Figs 42-46) and left valva (Figs 47-54) of each of the eight voucher specimens (4 x Morph type 1 and 4 x Morph type 2), showed that these structures were variable and, therefore, could not be used to discern morph types within the eight specimens.

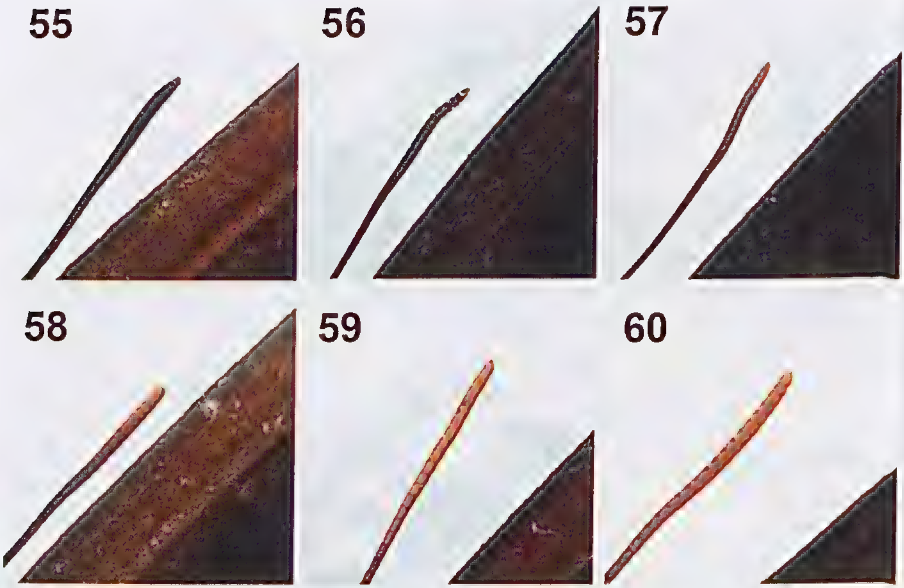
The phalli (Figs 38-41) (*i.e.* two Morph type 1 and two Morph type 2) were overall similar in shape but the degree of variation was dependant on how far the cornuti were extended (Figs 38-41). The shapes of the tips of the sacci in particular were variable including their length, but the variation in length might be relative to the size of the butterfly (Figs 42-46). In addition, overall shapes of the sacci were comparable only when viewed at the same angle and this was difficult to standardise when viewed microscopically. The valvae examined were mostly similar in overall shape (Figs 47-54) but their apical tips (claspers) were variable in their acuteness, with some more rounded (Figs 47, 50, 53) than others.



Figs 38-46. *Euploea batesii* 'complex', male genital armature: (38-41) ventral view of phallus to scale, all phalli approximately 4.5 mm long: (38, 40) Morph type 1 = *E. b. batesii*: (38) Brown R., nr Port Moresby, [Central Province); (40) Yapen, Irian Bay, 1995; (39, 41) Morph type 2 = *E. resarta* **stat. rev.**: (39) Sambio Mumeng, [Morobe Province], -.i.1985; (41) Bulolo, [Morobe Province], -.v.1985. (42) ventral view of genitalia including saccus, total length approximately 5 mm, Morph type 1 = *E. b. batesii*, Brown R. nr Port Moresby. (43-46) dorsal view of saccus to scale: (43, 45) Morph type 1 = *E. b. batesii*: (43) Brown R., nr Port Moresby; (45) Yapen, Irian Bay, 1995; (44, 46) Morph type 2 = *E. resarta* **stat. rev.**: (44) Sambio Mumeng, [Morobe Province], -.i.1985; (46) Bulolo, -.v.1985.



Figs 47-54. *Euploea batesii* 'complex', male genital armature (lateral left view of left valva [clasper] with tegumen and uncus removed [dorsal surface uppermost]), all valvae approximately 2 mm high: (47, 49, 51, 53) Morph type 1 = *E. b. batesii*: (47) Dauan I., Torres Strait, 2.i.2010; (49) Dauan I., 8.i.2010; (51) Brown R., nr Port Moresby [Central Province]; (53) Yapen, Irian Bay, 1995; (48, 50, 52, 54) Morph type 2 = *E. resarta* **stat. rev.**: (48) Murray (Mer) I., Torres Strait, 29.iii.-4.iv.1986; (50) Murray I., 29.iii.-4.iv.1986; (52) Sambio Mumeng [Morobe Province], -.i.1985; (54) Bulolo [Morobe Province], -.v.1985.



Figs 55-60. *Euploea batesii* 'complex', proportions of antennal length fulvous in colour (figures not to scale): (55, 56) fulvous colour <10% of antennal length: (55) Murray (Mer) I., 9.iii.1995, ♂, Morph type 2 = *E. resarta* **stat. rev.**; (56) Mer I., em. 11.iii.2011, ♂, Morph type 1 = *E. b. batesii*. (57, 58) fulvous colour 15-25% of antennal length: (57) Murray I., 29.iii.-4.iv.1986, ♀, Morph type 3 = *E. resarta* form *squalida* **stat. rev.**; (58) Mer I., em. 6.iii.2011, ♀, Morph type 1 = *E. b. batesii*. (59, 60) fulvous colour *circa* 40% of antennal length: (59) Dauan I., 16.i.2011, ♀, Morph type 1 = *E. b. batesii*; (60) Murray I., 22-25.iv.1989, ♂, Morph type 1 = *E. b. batesii*.

In addition, examination of specimens showed that the distal flagellomeres of the antennae, in both older and relatively fresh specimens and inclusive of the three morph types, were fulvous in colour (Figs 55-60), not black as in all but one other *Euploea* spp from Torres Strait. The extent of this fulvous colouring varied from being just the antennal tips (Figs 55-56) to the approximate terminal 35-45% of the antennal lengths (Figs 59-60).

Discussion

Precis of the biogeography of Torres Strait and eastern Papua New Guinea

The geological histories of the Torres Strait islands, Papua New Guinea and the Solomon archipelago are complex (Parsons 1998). Willmott (1972) indicated that northern Queensland (*i.e.* Cape York), the southern Torres Strait islands (*e.g.* Muralug [Prince of Wales] and Moa Is) and the top western Torres Strait islands to the north, *i.e.* Iama, Gabba and Dauan, have a similar geology, being composed of Carboniferous granite and acid volcanic rocks. This same granite rock 'basement' appears again as a granite boulder cluster at Mabaduan on the southern coastline of Papua New Guinea just north-east of Dauan I., then reappears further north several kilometres inland as the Oriomo Plateau, a low plateau mostly less than 50 m above sea level. Since around 10,000 years ago, the intervening areas between Cape York and the Oriomo Plateau have been inundated by Torres Strait and, in southern Papua New Guinea, covered by an alluvial terrace which is low and swampy (Willmott 1972). Prior to this, a prolonged Quaternary connection existed between New Guinea and Australia (Cranston and Naumann 1991). Therefore, based on the evidence of Willmott (1972) that Papua New Guinea and Cape York were once joined along this granite 'basement', it is not surprising that the butterfly fauna of the Torres Strait islands contains a mixture of Australian and Papua New Guinea faunal elements (Kitching and Dunn 1999, Braby 2000, unpublished data).

In contrast, the geology of Mer and its two associated islands Dauar and Waier (constituting the Murray Island group), in eastern Torres Strait, are thought to be the remnants of old volcanic activity of the Upper Carboniferous Period (Willmott 1972). While Mer I. is presently well isolated from the western Torres Strait islands and Papua New Guinea, components of the butterfly fauna recorded from the island indicate a link to eastern mainland Papua New Guinea, away from the granite based Oriomo Plateau (which lies directly north of Dauan Island).

Of the Mer I. butterfly fauna, several New Guinea taxa that occur on the island have not been recorded elsewhere in Torres Strait, including Mer's neighbouring volcanic islands of Erub (Darnley) and Ugar (Stephens). In addition to Morph types 2 and 3 of the *E. batesii* 'complex', which are only known to occur in Torres Strait on Mer I., several other butterfly taxa also appear to occur in Torres Strait only on Mer I. The occurrence of these taxa suggests that the island's butterfly fauna might be derived from eastern Papua New Guinea.

These other butterfly taxa are: *Nothodanis schaeffera caesius* (Grose-Smith, 1894) (Lycaenidae) (Lambkin and Knight 1990, Meyer *et al.* 2005), which occurs sporadically throughout mainland Papua New Guinea (Parsons 1998); *Hypolimnas antilope mela* Fruhstorfer, 1903 (Nymphalidae) (with one female specimen also recorded from Masig (Yorke) I., Torres Strait: Wood 1987a, b, Lambkin and Knight 1990) is rarely encountered in Papua New Guinea (Parsons 1998); *Melanitis constantia* (Cramer, 1777) (Nymphalidae) (Johnson *et al.* 1994), which is again widespread throughout mainland Papua New Guinea but rarely observed (Parsons 1998); and, in particular, *Euploea modesta lugens* Butler, 1876, (a single male recorded by Meyer *et al.* (2004) on Mer I.), whose distribution is otherwise restricted to the hinterlands of Port Moresby, Central Province (Parsons 1998, Meyer *et al.* 2004). Curiously, *Tellervo zoilus digulica* Hulstaert, 1924 (Nymphalidae), another butterfly taxon known only in Torres Strait from Mer I. (Johnson *et al.* 1994, Braby 2000) but, enigmatically, outside Torres Strait appears restricted to the Bensbach and Morehead River regions in the Western Province of Papua New Guinea (Parsons 1998), both locations not far from Dauan I.

With regard to the *E. batesii* 'complex', it extends east of the New Guinea mainland throughout the Solomon archipelago, where observed trends with its distribution and polymorphism are difficult to interpret, although different island populations are phenotypically constant (M. De Baar pers comm.). Similarly, Carpenter (1953) found this in his review of *Euploea* in Micronesia, Melanesia, Polynesia and Australia, where he found conundrums when attempting to elucidate the biogeography of the Solomons.

Interestingly, in the east of the Solomons, *E. b. ackeryi* Tennent, 2001, which occurs exclusively on Ulawa Island (Fig. 37), resembles nominotypical *E. batesii*, *i.e.* Morph type 1 from western New Guinea (Tennent 2001). In addition, *E. b. kunggana* Carpenter, 1953 from Rennell Island (Fig. 37), which is the most southerly island in the Solomon archipelago, is noticeably different from all other populations occurring northward through the archipelago but, in general, most resembles the well-spotted *E. b. resarta* (Morph type 2) from eastern mainland Papua New Guinea (including the Louisiade and D'Entrecasteaux island groups) (Fig. 37). When discussing this, Carpenter (1953) postulated that the well-spotted butterflies generally occurring on Rennell I., including *E. b. kunggana*, show a closer affinity with the butterflies of the eastern tip of mainland Papua New Guinea (*i.e.* Central, Oro and Milne Bay Provinces) (Fig. 37) and may have originated from this region, rather than via the main Solomon archipelago north of Rennell I.

Alternatively, Ackery and Vane-Wright (1984) and Tennent (2002) suggested that the well-spotted butterfly species occurring on Rennell Island, including *E. b. kunggana*, might be part of a Müllerian mimicry complex that might play a role in the phenotypic appearance of danaines on the island.

Additionally, Ackery and Vane-Wright (1984) reported on the danaid populations occurring on the islands in the Louisiade Archipelago, south-east of Milne Bay, and listed *E. b. rotunda* (Morph type 1) on the Conflict Is group and *E. b. resarta* (Morph type 2) on Nivani, Misima and Tagula Is (Fig. 37). This archipelago stretches partly across the southern extremity of the Solomon Sea almost directly in line with Rennell I. (Fig. 37). In a similar vein, Tennent (2001) commented that *E. b. ackeryi* resembled dark, unspotted *E. b. batesii* (Morph type 1) from New Guinea and that it was quite different from all the races of *E. batesii* proximal to it along the Solomon archipelago.

Therefore, in Torres Strait, a biogeographical pattern exists with island populations of the butterfly on the western islands, Dauan and Iama, being unspotted, as with populations occurring across most of New Guinea. This pattern supports the possible link in the geology of Dauan (Fig. 62) and Iama (Fig. 63) Islands with those of the Oriomo Plateau directly north in the

Western Province of southern Papua New Guinea. Similarly, Mer I. (Fig. 61) in the east has a mix of morph types similar to populations from the east of mainland Papua New Guinea. Occurrence of these morph types on Mer I., including those of other butterfly species recorded only in Torres Strait on Mer I., also indicates a possible geological link between Mer I. and the provinces to the east and north of Port Moresby in Papua New Guinea. Further studies of the butterfly fauna of the northwestern Torres Strait islands, including Gabba I. (which lies between Dauan and Iama Is) (Fig. 64), and the fauna of the southern and eastern provinces of Papua New Guinea, may offer further empirical evidence to support this link.

Figs. 61-64. Torres Strait islands: (61) Mer (northeastern aspect); (62) Duaun (southeastern aspect); (63) Iama (southern aspect); (64) Gabba (eastern aspect).

Life history and biology

The life history and host plant of Morph type 1 of the *E. batesii* 'complex' in Torres Strait were previously unknown. The larval host plant, *Parsonsia velutina*, is widely distributed throughout Torres Strait and southern and eastern Papua New Guinea (Atlas of Living Australia 2013, G. Sankowsky unpublished data), so it is possible that this species may be the host plant for Morph type 1 of the *E. batesii* 'complex' throughout these regions. In Papua New Guinea, Szent-Ivany and Carver (1967) reported *E. b. funerea* Butler, 1878 (which resembles *E. b. squalida*) from Port Moresby to be a frequently observed taxon whose larvae were found commonly on *Nerium oleander*, but they did not provide a description of the larva. In Torres Strait, immature stages of the *E. batesii* 'complex' have not been observed on *N. oleander* despite careful surveillance of plants over several decades (unpublished data). The only reference to *N. oleander* as a *Euploea* larval host plant in Torres Strait is by Johnson and Valentine (1997), who reared adults of *E. alcathoe misenus* Miskin, 1890 (as *E. a. monilifera* [Moore, 1883]) from pupae collected on *N. oleander* on Dauan I.

Parsons (1998) illustrated the fourth and fifth instars of the *E. batesii* 'complex' from material collected on *Parsonsia lata* from the Bulolo district, Morobe Province, Papua New Guinea. Although very similar to the two instars of Morph type 1 described in this work and based on a single record, there are some subtle differences between the larvae from Bulolo (Parsons 1998) and those from Mer I. Based on the illustration in Parsons (1998) and the final instar larvae collected and reared on Mer I., it appears that the lengths of all the filaments of the final instar larvae from Mer I. are approximately twice the width of the body of the larva (Figs 6-7), whereas the filaments of the final instar larva illustrated in Parsons (1998) are almost all less than the width of the body, except the mesothoracic pair which is a little more than the width of the body. The filaments of the fourth instar larva illustrated again appear to be shorter overall in the Bulolo specimen (Parsons 1998) than in specimens from Mer I. (Fig 5), while the Bulolo specimen illustrated is a much brighter orange (Parsons 1998) than any fourth instar larva observed from Mer I., which were all dull yellow-orange in colour (Fig 5). Unfortunately, Parsons (1998) did not specify the wing pattern morphology of the adults that he reared from these larvae and there is only one illustration (used in Ackery and Vane-Wright 1984 and Parsons 1998) available for comparison, so it is not known which morph type he reared from these particular larvae. Considering that Bulolo lies in the area where all three morph types occur, the subtle differences of the larvae noted between the two locations, and in view of Parsons (1998) indicating the extreme variability of *E. batesii* from the Bulolo area, it is possible that the adult butterflies reared from these larvae might have been Morph type 2 or 3, *i.e.* resembling *E. b. resarta* or *E. b. squalida*, with white or 'obsolescent' spots, but further information is required before any inference can be made. In any case, the distinctive appearance of final instar larvae from Mer I. and Bulolo, especially their charcoal black colour devoid of any colour banding, has not been observed elsewhere in final instar larvae of *Euploea* spp occurring in New Guinea and Australia (Saguru and Fukuda 1997, 2000, Parsons 1998, Braby 2000) and might be characteristic of the *E. batesii* 'complex'.

Ackery and Vane-Wright (1984) documented the plant species known to attract adult danaines, predominantly as a source of pyrrolizidine alkaloids. Here, I record for the first time a pyrrolizidine alkaloid source for danaines in Torres Strait, viz. *Heliotropium foertherianum*, for the *E. batesii* 'complex' (three morph types), *E. a. amycus*, *E. t. tulliolus* and *T. h. hamata*. *Heliotropium foertherianum* is known to contain pyrrolizidine alkaloids and is recorded in the literature as readily attracting danaines in the Pacific (Ackery and Vane-Wright 1984, Tennent 2002b, Patrick and Patrick 2012).

Taxonomy of the E. batesii *'complex'*

From the early days, the Northern Moluccas remained the type location and the types appeared to be the only known specimens of nominotypical *E. batesii* (Edwards *et al.* 2001). As a result of confusion with the types, Fruhstorfer (1910) did not illustrate nominotypical *E. batesii* in his treatise but chose to illustrate *E. b. pinaria* Fruhstorfer, 1910 from Waigeo as a representative of the type. Subsequently, a plethora of names, many originally described as species, was given to populations from mainland New Guinea and its adjacent islands. Excluding the far east of mainland Papua New Guinea, the most recently assigned names are: *E. b. arcana* Talbot & Le Cerf, 1925 from Seram, Ambon and Buru; *E. b. pinaria* from Waigeo; *E. b. ebinena* Butler, 1866 from the Aru islands; *E. b. incerta* Joicey & Noakes, 1915 from Biak (including Yapen) (Fig. 16); *E. b. gorgonia* Hulstaert, 1924 and *E. b. mimica* Fruhstorfer, 1910 from western New Guinea; and *E. b. publilia* Fruhstorfer, 1910 from Astrolabe Bay, Madang Province, Papua New Guinea (Fruhstorfer 1910, Carpenter 1953, Ackery and Vane-Wright 1984, Parsons 1998). Based on their descriptions, the wing patterns of these populations from most of mainland New Guinea and its close outlying western islands are, for the most part, similar, if not essentially the same as the description of the type of *E. batesii* (Felder and Felder 1865) (*i.e.* Morph type 1) (Fruhstorfer 1910, Barrett and Burns 1951, Carpenter 1953, Ackery and Vane-Wright 1984, Parsons 1998). In contrast, white-spotted and 'obsolescent' populations appear to be restricted to the far east of mainland Papua New Guinea, its close neighbouring islands and Mer I. in Torres Strait.

Fruhstorfer (1910) was the first to reduce the number of species names within the complex, indicating that *E. batesii* occurred as an unspotted species across most of the New Guinea island but at the same time describing several subspecies, possibly succumbing to the trend of using the trinomial system of taxonomy that had just gained popularity by the early 20th Century (Braby *et al.* 2012). In addition, Fruhstorfer (1910) synonymised many of the names in the east of Papua New Guinea, retaining *E. resarta* and *E. funerea* as species. Following this, Waterhouse and Lyell (1914) and Waterhouse (1932) referred the Torres Strait population to *E. b. belia*, which was in accord with Fruhstorfer (1910), while Corbet (1943) referred all populations of the *E. batesii* 'group' to one single species occurring from the Moluccas to the Solomons. Carpenter (1953) later grouped the populations into geographical races, effectively subspecies, as part of a complex. Most recently, Ackery and Vane-Wright (1984) followed Corbet (1943) and Carpenter (1953) and maintained their synonymy, placing them in a single species, *i.e. E. batesii*.

In the current study, examination of the genital armature of Morph types 1 and 2 showed no consistent differences. Similarly, Corbet (1942) examined the genitalia of several species-groups of *Euploea* and concluded that differences in genital armature were not discernible between closely related species. Moreover, Talbot (1943) determined that there were no differences between the genital armature of *E. batesii* (he did not specify the origins of the specimen[s] he examined) and *E. honesta* Butler, 1882 (*E. b. honesta*) from the Solomons, despite there being noticeable and consistent differences in the adult wing pattern.

Interestingly, the noticeably fulvous colouring of the distal flagellomeres of the antennae on all specimens examined of the *E. batesii* 'complex' from New Guinea and Torres Strait (Figs 55-60) provides another character to assist in distinguishing specimens of female *E. batesii* from females of several similar-looking species in Torres Strait, viz. *E. sylvester* (Fabricius, 1793), *E. algea* (Godart, [1819]) and *E. alcathoe* (Godart, [1819]). Furthermore, examination of specimens of all species of *Euploea* from Torres Strait (in TLIKC) showed that this antennal character was shared only with *E. netscheri nerana* Fruhstorfer, 1910 (31 specimens examined from Dauan [10♂♂, 20♀♀] and Saibai [1♀] Islands). Thus, despite the fulvous distal flagellomeres of the antennae being a helpful character in distinguishing female specimens of the *E. batesii* 'complex' from most other similar-looking *Euploea* species, this character may make it difficult to separate them from female *E. netscheri* Snellen, 1889. This particular character may indicate a closer relationship between *E. batesii* and *E. netscheri* than is currently thought (Ackery and Vane-Wright 1984). The relationship between these two taxa might be better understood once the life history and, in particular, the final instar larva of *E. n. nerana* are known.

Distribution in Papua New Guinea and Torres Strait

In the far east of mainland Papua New Guinea, numerous names have been applied to populations of the *E. batesii* 'complex' (with six subspecies described), in which wing pattern morphology seems to be highly variable even in discrete locations, *i.e.* specimens range from unspotted black or dark brown forms (Morph type 1) to well spotted forms (Morph type 2), often with both forms and intermediate-looking forms (*i.e.* Morph type 3) occurring at the same locality (Table 1). Carpenter (1953) looked at the variation within these names and accordingly treated several taxa (*E. b. funerea* and *E. b. squalida* from Port Moresby, Central Province; *E. b. turbonia* Fruhstorfer, 1910 from Simbang, Morobe Province; and *E. b. murena* Fruhstorfer, 1911 from Yule Island, Central Province) as junior synonyms of *E. b. resarta*, the Holotype being from Port Moresby (Butler, 1876). Similarly, as discussed earlier, *E. b. publilia* from Astrolabe Bay (a predominantly dark brown to black form) and *E. b. rotunda* van Eecke, 1915 (which is also dark brown to black), are known from Mekeo (type locality) and Yule Island (both Central Province) respectively (Parsons 1998), with Yule I. being the same type locality as for *E. b. murena* (Fruhstorfer, 1911). Both Mekeo and Yule I. are close to Port Moresby so, according to the correlation of Carpenter (1953), it is probable that *E. b. rotunda* should also be treated as a synonym of *E. b. resarta.*

In Australia, *E. b. belia* was described from three males and five females originating from 'Cape York' (1♂, 1♀ AM), Erub (Darnley) I. (1♀ AM), Mer (Murray) I. (1♂ AM) and 'Australia' (1♂, 1♀ MM) (Peters 1971) (the depository of the remaining 2♀♀ is unknown). The wing pattern of almost all of these early Australian specimens is dark brown to black without spots (Morph type 1), strongly reminiscent of *E. b. batesii.* As reported earlier, the exception is the male allegedly collected at Cape York and illustrated in Waterhouse and Lyell (1914), whose wing pattern morphology is consistent with Morph type 3, *i.e.* with white spots and bars overlaid with dark ground colour scales (as per Figs 29-32). Later, it seems that Waterhouse (1932) had doubts about the authenticity of Cape York as a location for *E. batesii* as he redefined the species as only occurring within Australia on Darnley (Erub) and Murray (Mer) Islands, Torres Strait. Perhaps the Cape York records are similar to those of several other butterfly specimens from this early period that were also purportedly collected from Cape York and Thursday Island, but were found later to originate, in all likelihood, from New Guinea or further afield (Waterhouse and Lyell 1914, Meyer *et al.* 2004, Lambkin 2005). Thus, in all probability, these two Australian locations were points of export for these consignments of natural history specimens, not the places of capture.

In Torres Strait, specifically on Mer I., the *E. batesii* 'complex' occurs as the three morph types (described as subspecies); *i.e.* Morph type 1 described as *E. b. belia* (Figs 13-15, 17-20), Morph type 2 (known as *E. b. resarta*) (Wood 1987a, Lambkin and Knight 1990) (Figs 21-28) and Morph type 3 (nearest to *E. b. squalida*) (Figs 29-32). On other Torres Strait islands (*i.e.* Erub, Iama and Dauan) *E. batesii* is only known as Morph type 1. Wood (1987a) found all three subspecies (or morph types) on Mer I. and, based on this, he treated *E. b. belia* as a junior synonym of *E. b. resarta.* Thus, from that time, all three morph types of the *E. batesii* 'complex' were considered, at least on Mer I., to be *E. b. resarta* (Braby 2000). Similarly, this study has shown that Morph type 3 occurs only in areas where Morph types 1 and 2 occur sympatrically. These areas appear to be exclusively eastern mainland Papua New Guinea and Mer I. in Torres Strait.

Morph type 1 of the E. batesii *'complex' and* Parsonsia velutina

On searching for immature stages of the *E. batesii* 'complex' on Mer I., *P. velutina* was the only species of *Parsonsia* found (and is the only species recorded: Atlas of Living Australia 2013), and only on this species were found immature stages, which solely produced adults of Morph type 1. However, it is possible that either an unrecorded species of *Parsonsia* or another species in the Apocynaceae (with four others recorded from the island: Atlas of Living Australia 2013) may constitute the larval host of the maculated forms of the *E. batesii* 'complex' (*i.e.* Morph types 2 and 3), which occur sympatrically with Morph type 1 on the island.

Conclusion

The geographical distribution and wing pattern morphological stasis of Morph type 1, which occurs in a continuum across New Guinea with an abrupt and exclusive modification in the far east of the island where Morph types 2 and 3 occur with it, is problematic in its interpretation, especially in terms of differentiating the morph types as subspecies (as per Fruhstorfer (1910) and Carpenter (1953)). This is especially the case when attempting to apply the most fundamental premise of the subspecies model to this unique distribution, the premise in question being based on allopatric populations requiring geographic isolation to be regarded as subspecies. In a recent review of the utility of subspecies as a taxonomic unit, Braby *et al.* (2012) concluded that defining species was problematic because of attempts to apply the species concept in nature. Their review concluded that, when applying the species concept, multiple lines of evidence are preferable.

In view of the data presented here on the *E. batesii* 'complex' in the New Guinea region, this study provides evidence indicating that '*E. batesii*' does not constitute a single species on the island of New Guinea. The data further suggest that the *E. batesii* 'complex' occurring through the major islands and archipelagos east of New Guinea, in particular the Solomon Islands, also constitutes more than one species. These lines of evidence are:

Specimens of Morph type 1 (taxon *batesii*) and Morph type 2 (taxon *resarta*) can clearly be differentiated based on wing pattern morphology, *i.e.* specimens of *batesii* are black or dark brown without white spotting (immaculate), while specimens of *resarta* are also black or dark brown but have varying degrees of bright white spots or bars (maculation), these spots sometimes overlayed and obscured with dark brown ground colour scales (taxon *squalida*);

The stasis of the dark immaculate taxon (Morph type 1) that occurs across New Guinea and several islands in Torres Strait;

The high frequency of polymorphism that includes the well-spotted taxon Morph type 2 (taxon *resarta*) and Morph type 3 (taxon *squalida*), which occur uniquely together with the dark immaculate form (Morph type 1) only in the far east of mainland Papua New Guinea and on Mer I. in the eastern sector of Torres Strait;

Life history data showing that Morph 1 types only arise from Morph 1 type mothers;

Morphologically consistent larval characters of material reared from Mer I., which includes the unique colouring of the final instar larva and larval filament length, being consistent with Morph 1 type adults; and

Apparently longer filament lengths of larvae, in particular the final instar from Mer I., than filaments of the same from Bulolo in eastern Papua New Guinea.

Based on the evidence presented in this revision, it is proposed that *E. resarta* **stat. rev.** be revised to species status. In addition, the results of the study indicate that *E. batesii* and *E. resarta* are closely related in terms of their genital armature, the elongate stripes in and above space 1b on the underside of the forewings and the fulvous colour of the distal flagellomeres of the antennae. Moreover, the distributional data show that these two species form a sympatric zone in eastern mainland Papua New Guinea (and perhaps also in the D'Entrecasteaux and Louisiade Archipelagos) and on Mer I. in Torres Strait. Whereas *E. b. batesii* occurs across the island of New Guinea and throughout Torres Strait as a distinctive stand-alone species, *E. resarta* (including f. *squalida*) in contrast appears to exist only in the east, where it occurs sympatrically with *E. b. batesii*. These unique distributions might be determined by larval host plant preferences.

Finally, based on evidence provided here, populations of the *E. batesii* 'complex' (Morph type 1) occurring on mainland New Guinea and its outlying islands and in Torres Strait (subspecies *E. b. arcana*, *E. b. ebinena*, *E. b. gorgonia*, *E. b. incerta*, *E. b. mimica*, *E. b. pinaria*, *E. b. publilia*, *E. b. rotunda* and *E. b. belia*) are placed as **new synonyms** of *E. b. batesii*. Until further research is undertaken on the distribution, life histories and molecular character of the *E. batesii* species 'complex' in New Guinea, Torres Strait and beyond, an explanation for the distribution and frequency of the morphological types observed in mainland Papua New Guinea and Torres Strait is that of a single monotypic species (*E. b. batesii*) in New Guinea that overlaps in distribution with a polytypic species (*E. resarta*) in eastern Papua New Guinea and on Mer I. in Torres Strait. Within its distribution, *E. resarta* is polymorphic and varies from specimens with a high degree of white spotting or maculation to relatively dark individuals with vestigial spotting, or having white spots that are obscured under a layer of dark coloured ground scales (form *squalida* **stat. rev.**).

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